Tail Display Intensity is Restricted by Food Availability in an Asian Agamid Lizard (*Phrynocephalus vlangalii*)

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Abstract To ascertain the function of signals, we have to first uncover the reasons behind signal variation. There are several potential driving forces, including background noise, predation cost, receiver perception, and energy limitations. The energy limitation hypothesis assumes that individuals trade off signal intensity and energy expenditure according to resource condition, while variation of signal intensity likely associates with food availability. This hypothesis has been evidenced by a great number of researches on vocal signals, but no studies evaluated the influence of food availability on motion visual signal in lizards. Here we used an Asian agamid lizard *Phrynocephalus vlangalii* and examined the effect of food availability on tail display intensity. We designed two food restriction treatments as well as a nature control treatment, and quantified individual tail display speed and display duration under different food availability conditions. Consistent with our prediction, our results showed that males significantly reduced their average tail display speed and maximum display speed in both food restriction treatments when compared to nature control condition. Therefore, our study provides direct evidence that lizards would trade off their display intensity according to the food condition, suggesting tail display is energetically costly and likely provides honest information on individual body condition and resource hold potential.

1. Introduction

Signal variation plays crucial roles in animal communication, because of its relevance on signal function (Martin, 2013). Information regarding individual body conditions and resource hold potentials can be transmitted among conspecifics in virtue of signal variation (Docherty *et al*., 1995; Howard *et al*., 1998; Brepson *et al*., 2013; Humfeld, 2013). This is particularly true for motion visual signals, which requires an intimate coordination among different body organs and likely reflect individual ability in resource and social competition (Fleishman, 1992; Vanhooydonck *et al*., 2005; Mowles *et al*., 2017). For example, variation of claw waving in male fiddler crab *Uca mjoebergi* reflects individual sprint speed (Mowles *et al*., 2017), while variation of dewlap size in *Anolis* lizards manifests individual bite force (Vanhooydonck *et al*., 2005). To ascertain the function of signals, we have to first figure out the reasons behind signal variation.

Many hypotheses were proposed to address the reasons behind signal variation, including background noise, predation risk and energy limitation (Zuk and Kolluru, 1998; Peters and Christopher, 2003). The background noise hypothesis assumes that signal variation is aimed to cope with the problem of background noise (Peters *et al*., 2008; Kaiser *et al*., 2009; Hanna *et al*., 2014; Halfwerk *et al*., 2016). Individuals would modify their signal intensity to overcome the interference from background noise, e.g. waterfalls, wind, and urban noise (Ord *et al*., 2007; Luther and Gentry., 2013; Halfwerk *et al*., 2016). The predation risk hypothesis assumes that signal variation plays crucial roles in camouflage; individuals would modify their signal

Xinxin ZHU *et al.*
Variation of Tail Display Intensity
in *Phrynocephalus vlangalii*

No. 3   241

variation to alleviate the predation risk (Simon, 2007; Steinberg *et al.*, 2014). The energy limitation hypothesis proposes that signal variation reflects the status of individual energy condition, and thus there would be a trade-off between signal intensity and individual energy expenditure, in particularly for motion visual signal, as it requires an intimate coordination among different body organs (Endler, 1993; Kim *et al.*, 2008; Takeshita *et al.*, 2018). Display signals often exert significant influence on individual energy metabolism and have high requirements on individual physical condition (Sally *et al.*, 2003; Christophe *et al.*, 2013; Doubell *et al.*, 2017). For example, male African clawed frogs *Xenopus laevis* decrease call rate under high food constraint (Wang *et al.*, 2019). High speed drumming display in male wolf spiders *Hygrolycosa rubrofasciata* reduces individual weight and intensifies individual mortality rate (Mappes *et al.*, 1996). To alleviate the effect of energy costs, individuals often modulate their signal intensity to adapt to their energy condition.

Compared with background noise and predation risk hypotheses, the effect of energy limitation on signal variation remains largely unclear, in particular for motion visual signals in lizards. The Qinghai toad-headed agamid lizard, *Phrynocephalus vlangalii*, a common and widespread viviparous lizard at the Qinghai-Tibetan plateau, provides an excellent system testing the association between motion visual signal modulation and energy limitation. Both male and female lizards use complex tail displays in social communications, including male-male competition, male courtship, female-female competition, and female mate defense (Figure 1 a, Qi *et al.*, 2011a; Peters *et al.*, 2016; Wu *et al.*, 2018). Tail coil and tail lash are the two main display components in *P. vlangalii* (Peters *et al.*, 2016), and variation of tail coil and tail lash largely depends on the individual anaerobic metabolism capacity (Zhu, unpublished data). We also found that variation of tail coil and tail lash informs individual performance and burrow quality (Qiu, unpublished data). Both male and female are territorial and defend certain home range area around their burrow. They would stay near the burrow entrance, and initiate a quick predation as soon as the insects land on the grass two meters away (Qi *et al.*, 2011b, 2012; Wu *et al.*, 2015). As a high elevation species, the availability for food are very limited, individuals likely have a trade-off between food availability and display intensity to maintain the normal metabolism and reproduction (Aspey *et al.*, 1983; Briffa *et al.*, 2001; Dammhahn *et al.*, 2018).

In this study, we test the applicability of energy limitation hypothesis in motion visual signal. We achieved the manipulation of food availability through restriction on individual foraging behavior, which serves as an important method for food availability restriction in the field condition. According to trade-off between signal intensity and individual energy expenditure, we predicted that *P. vlangalii* would reduce their display intensity when food availability was low.

2. Materials and Methods

2.1. Study site   We conducted our experiment at the Xiaman Conservation Station in the Zoige Wetland Nature Reserve (33.71389° N, 102.48543° E, elevation 3475 m a.s.l), northeast Sichuan Province, China. *Phrynocephalus vlangalii* in this area occurs in sand dunes surrounded by grassland, with a population density of approximately 3000 lizards/ha and a sex ratio (female/male) of 1.76/1 in mating season (Wu *et al.*, 2002; Wu, 2003). The active season of lizards in this area lasts from May to late August, with mating occurring from early May to late June, and young emerging in late August and early September, with a clutch size ranging from 1 to 4 (Wu *et al.*, 2015). The vegetation around lizards' burrow is predominantly composed of three grass species (*Kobresia humilis*, *K. prattii* and *Elymus natans*) and a shrub (*Salix sclerophylla*) (Qi *et al.*, 2011a). The climate in this area is characterized by a short spring and summer (four months, from April to July) and a long autumn and winter (eight months, from August to March of the following year) (Chen *et al.*, 1996).

2.2. Experiment design   Two food restriction treatments, food restriction one (FRO) and food restriction two (FRT), as well as a nature control treatment, were designed to examine the effect of food availability on tail display intensity during breeding season that occurs from May and June (Figure 1 b). In FRO, we removed the bottom of plastic case (60 cm × 45 cm × 34 cm), and replaced it using fishing net. We then put the case with bottom up around the lizards' burrow and restricted the lizards' foraging behavior. In FRT, we used the similar plastic case, but did not replace the removed bottom with fishing net. Therefore, the similarity of the FRO and FRT is that the focal lizard could venture out of its burrow and move in a restricted area of 60 cm × 45 cm, but could not approach the plants where the insects likely to land on and forage efficiently as in a nature condition (Qi *et al.*, 2012). We assume that insect availability in nature control is higher when compared with those in FRO and FRT, while insect availability of FRT is higher than FRO due to the absence of fishing net. This is designed according to the foraging
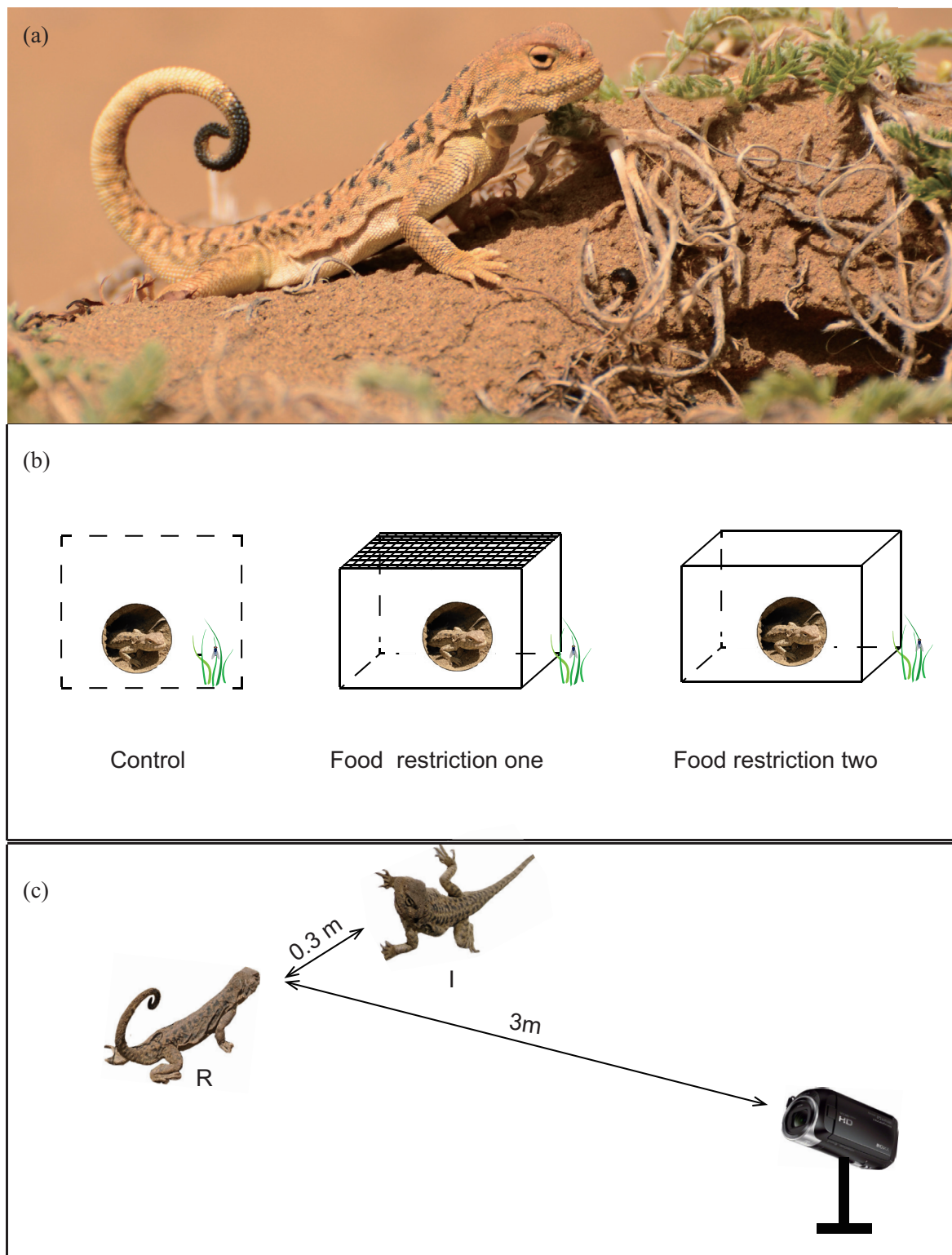
Figure 1 Diagrammatic drawing of experimental design. (a) an image of male tail display around its burrow in *Phrynocephalus vlangalii*; (b) general view of nature control, food restriction one (FRO) and food restriction two (FRT); (c) general view of display collection process. R = Resident, I = Intruder. In FRO, we removed the bottom of plastic case (60 cm × 45 cm × 34 cm), and replaced it using fishing net. We then put the modified case with bottom up around the lizards' burrow and restricted the foraging behavior of lizards. In FRT, we used the similar case, but did not replace the removed bottom with fishing net. The similarity of the two treatments is that the focal lizard could venture out of its burrow and move in a restricted area of 60 cm × 45 cm, but could not approach the plants where the insects likely to land on and forage efficiently as nature condition. We assume that insect availability in nature control is higher compared with those in FRO and FRT, while insect availability in FRT is higher than FRO due to the absence of fishing net.

Xinxin ZHU *et al.*
Variation of Tail Display Intensity
in *Phrynocephalus vlangalii*

No. 3

243

behavior in *P. vlangalii* (Qi *et al.*, 2011a).

One day before trials, we searched the study area for resident males and captured them by noose. The body mass and snout-vent length (SVL) were measured respectively using an electronic scale (MAXN, precision 0.01 g) and a clear plastic ruler as soon as they were caught. We then released the resident to its burrow and marked the burrow using a chopstick. To reduce the likelihood of previous interactions between lizards, we captured intruder males from a different site three kilometers away.

A minimum of 24 h later, we returned to the marked male residents and tested their responses to male intruders under nature control treatment. We tethered an intruder male to approach the resident using a four meters' fishing rod. To allow the lizard move freely, we used a 40 centimeters' dental floss with one end tied around the waist of lizard and the other end attached to the fishing rod. Meanwhile, a video camera (50 frames per second, Sony HDR PJ670) was set up in front of the resident and recorded the display responses. We terminated the trial when resident stopped its display or stayed without displaying within a maximum of five minutes. At the conclusion of each trial, a ping-pong ball was immediately placed at the signaling site as a scale for display digitizing. After that, the focal lizard was randomly assigned a food restriction treatment (FRO or FRT, Figure 1 b). To avoid the lizards' escape, we inserted the edge of plastic case into the sand and buried its edge. To facilitate individual recognition, we marked the burrow using a numbered chopstick. After three days' food restriction (Yue *et al.*, 2012), we re-collected the tail display of focal lizard using the same method.

To avoid biasing display variation due to the intruder and camera, we standardized each trial from three aspects: 1) SVL and mass were matched between resident and intruder, allowing SVL differences between individuals as much as 0.4 cm and mass difference as much as one gram; 2) distance between resident and intruder was kept at approximately 30 cm; 3) distance between camera and resident was kept at three meters. To alleviate the stress, we did not catch the focal lizard a second time again after food restriction treatment. Each intruder was used in a maximum of three times and was released back to the capturing site to alleviate physiological stress.

2.3. Display digitizing   We used the DLT dv5 software in Matlab 2015b (MathWorks Inc., Natick, MA, U.S.A.) and followed the methods outlined by Hedrick (2008) in display digitizing. We first located the position of tail tip in successive frames to generate *x-y* coordinate data over time for each display. After that, we extracted

the average display speed, maximum display speed and display duration respectively for tail coil and tail lash. The definition of average display speed, maximum display speed and average duration was consistent with the description in Wu *et al.* (2018). Briefly, the average display speed was defined as the average distance moved by tail-tip within a specific period of time, while the maximum display speed was defined as the maximum distance moved by tail-tip during that time. The display duration was computed as the time period display sustained. As orientation of the lizard relative to the camera likely affect display speed quantification (Bian *et al.*, 2016; Wu *et al.*, 2018), we categorized each display as either facing towards/away from the camera or at right angles to the camera. Finally, we transformed the grid-based display variables to Euclidean distance using the ping-pong ball scale.

2.4. Statistical analysis   We included tail displays of 43 lizards in final analysis. Thirteen out of original 56 lizards were excluded, because of escaping from the plastic case, lack of morphological measurements, or failing to display during trials. A total of 220 display bouts were quantified, including 132 bouts in natural control (26 lizards), 36 bouts in FRO (8 lizards) and 52 bouts in FRT (9 lizards).

All statistical analysis was carried out in R version 3.6.0 (R Developmental Core Team, 2017). We used the *lmer* function from lme4 package to establish linear mixed models (Bates *et al.*, 2015). For models of average display speed and maximum display speed, we regarded average display speed and maximum display speed as dependent variables, while food availability treatment, display action and display view were considered as fixed factors, with lizard identity using as random factor. For model of display duration, we regarded display duration as dependent variable, while food availability treatment and display action were considered as fixed factors. To satisfy the assumption of linear mixed model, we conducted a log transformation for each independent variable before modeling. We also included possible interactions between fixed factors. In addition, we considered intruder and resident SVL as covariates to explain potential effect of lizards' body size. The *lmerTest* function was used to assess the significance of each factor (Kuznetsova *et al.*, 2016). We examined pairwise contrast from the model for significant main effect. Descriptive statistics were given as mean ± SE.

## 3. Results

The mean value of average display speed was 13.06 ± 1.06

cm/s, 9.38 ± 1.15 cm/s and 9.80 ± 1.37 cm/s, for natural control, FRO and FRT, respectively (Figure 2a). Significant association was found between average display speed and food availability treatment (Table 1). The average display speed in the natural control was significantly larger than both restriction treatments, while no difference was found between two food restriction treatments (Table 1, natural control – FRO: $t = -2.39$, $P = 0.018$; natural control - FRT: $t = -2.61$, $P = 0.011$; FRO - FRT: $t = 0.59$, $P = 0.56$).

The mean value of maximum display speed was 50.85 ± 2.69 cm/s, 40.24 ± 2.90 cm/s and 35.56 ± 2.89 cm/s, for natural control, FRO and FRT, respectively (Figure 2b). We found significant association between maximum display speed and food availability treatment (Table 2). The maximum display speed under natural control was larger than FRO, although the difference was not significant (Table 2, natural control - FRO: $t = -1.15$, $P = 0.25$). The maximum display speed in FRT was significantly smaller than natural control (Table 2, natural control - FRT: $t = -2.34$, $P = 0.028$).

The mean value of display duration was 4.13 ± 0.29 s, 4.79 ± 0.54 s and 3.88 ± 0.44 s, for natural control, FRO and FRT, respectively (Figure 2c). We found no association between display duration and food availability treatment (Table 3).

4. Discussion

We found evidence that *P. vlangalii* modify tail display intensity depending on food availability. In particular, average and maximum tail display speed decreased when lizards experienced food restriction. This result is consistent with our prediction according to energy limitation hypothesis. Similar results have been found in fiddler crap *U. lactea* and wolf spiders *Schizocosa ocreata*, in which ample food would makes courtship display more intensive (Kim *et al.*, 2003; Gibson *et al.*, 2012). Another case was found in three-spined stickleback *Gasterosteus aculeatus*, in which food deprivation reduces the courtship display intensity in male individuals (Candolin, 1999). The energy-dependent signal modulation was also found in other signal models. For example, in lizards *Lacerta viridis*, male individuals increase nuptial color brightness under high food condition (Mészáros *et al.*, 2017), while in male European tree frogs *Hyla arborea*, individuals supplied with additional food call more frequently than control males (Meuche and Grafe, 2009). Similar pattern was found in Silvereyes *Zosterops lateralis*, in which food supplement prolongs call duration and increase call frequency (Barnett and Briskie, 2006). The association between tail
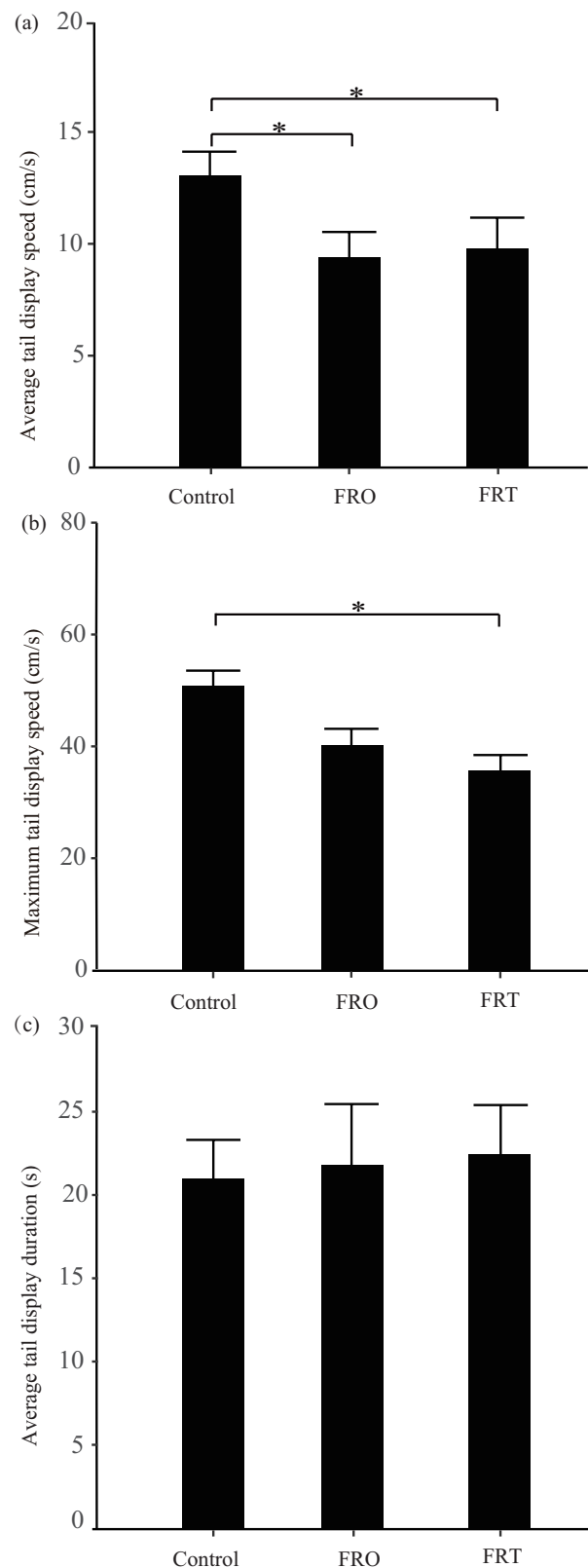
Figure 2 Mean value and standard error of three tail display parameters in *P. vlangalii*. (a) average tail display speed; (b) maximum tail display speed; (c) average tail display duration. Asterisk denotes significant effect between treatments (*P* < 0.05). FRO = food restriction one, FRT = food restriction two.

Xinxin ZHU *et al.*
Variation of Tail Display Intensity
in *Phrynocephalus vlangalii*

| No. 3 | 245 |

Table 1 Summary of linear mixed models examining variation of average display speed against treatment, action, display view and potential interactions. df_{Num} = numerator degrees of freedom, df_{Den} = denominator degrees of freedom with corrections based on the Satterthwaite approximation. Bold numbers denote significant effect.

Variable	Test of main effect				Paired contrast		
	df_{Num}	df_{Den}	F	P	t	df	P
treatment	2	49.36	6.09	**0.0043**			
food restriction one vs. nature control					−2.39	155.66	**0.018**
food restriction two vs. nature control					−2.61	75.69	**0.011**
food restriction one vs. food restriction two					0.59	133.38	0.56
action	1	177.10	387.16	**< 0.001**			
view	2	191.94	2.64	0.074			
reSVL	1	29.61	1.89	0.18			
inSVL	1	35.45	0.14	0.71			
treatment*action	2	179.89	0.79	0.46			
action*view	2	178.77	3.36	0.037			
treatment*view	4	161.38	0.93	0.45			

Table 2 Summary of linear mixed models examining variation of maximum display speed against treatment, action, display view and potential interactions. df_{Num} = numerator degrees of freedom, df_{Den} = denominator degrees of freedom with corrections based on the Satterthwaite approximation. Bold numbers denote significant effect.

Variable	Test of main effect				Paired contrast		
	df_{Num}	df_{Den}	F	P	t	df	P
treatment	2	51.5	5.61	**0.0063**			
food restriction one vs. nature control					−1.15	160.89	**0.25**
food restriction two vs. nature control					−2.34	81.35	**0.028**
food restriction one vs. food restriction two					−0.37	137.8	0.71
action	1	177.82	87.23	**< 0.001**			
view	2	196.64	2.07	0.13			
reSVL	1	32.12	0.44	0.51			
inSVL	1	37.98	0.016	0.90			
treatment*action	2	180.34	0.24	0.79			
action*view	2	179.18	1.43	0.24			
treatment*view	4	165.64	0.18	0.95			

Table 3 Summary of linear mixed models examining variation of display duration against treatment, action, display view and all potential interactions. df_{Num} = numerator degrees of freedom; df_{Den} = denominator degrees of freedom with corrections based on the Satterthwaite approximation. Bold numbers denote significant effect

Variable	Test of main effect			
	df_{Num}	df_{Den}	F	P
treatment	2	211	1.36	0.26
action	1	211	42.39	**< 0.001**
reSVL	1	211	2.4	0.26
inSVL	1	211	0.6	0.98
treatment*action	2	211	0.09	0.98

display intensity and food availability suggests tail display intensity could provide honest information on individual body condition and resources hold potential. Only individual with ample food could maintain high level of tail display intensity, thereby gain high dominance in mate competition and territory defense (Qi *et al.*, 2011a,

2012; Peters *et al.*, 2016).

There are several potential reasons on energy-dependent display modification in *P. vlangalii*. Individual *P. vlangalii* likely requires enough food to maintain the normal metabolism capacity and provides necessary energy associated with display. As a special kind of

signal, this display requires intimate coordination among different organs and hence likely has high requirements on individual food condition. Individual current body condition affects the structure of display signals (Kotiaho *et al.*, 1998; Scheuber *et al.*, 2003; Ritschard *et al.*, 2011; Gibson *et al.*, 2012). For example, in tungara frog *Physalaemus pustulosus*, male individuals without food supplement decrease call activity (Marler *et al.*, 1996). When food availability is low, individuals likely reduce display intensity to alleviate the negative impact from predation risk and immunocompetence (Bennett, 1980; Slavík *et al.*, 2017; Turbill *et al.*, 2019). For example, in fiddler crab *Austruca lacteal*, male individuals decrease the number of courtship waves when experiencing food-deprivation treatment (Takeshita1 *et al.*, 2018). Alternatively, individual *P. vlangalii* likely requires enough food to maintain muscle force associated with display intensity. Muscle force largely depends on the amount of muscle protein, which would be lost with the amino acid oxidation and /or carbon donation for gluconeogenesis (Wackerhage *et al.*, 2006; Atherton *et al.*, 2012). Individuals have to take a large number of amino acids from dietary protein (Wackerhage *et al.*, 2006; Atherton *et al.*, 2012). When food availability is low, the dynamic relationship between muscle protein and amino acid oxidation would be broken (Li and Goldberg, 1976), and lizards likely weaken the muscle capacity and reduce the display intensity.

We admitted that our food restriction treatment have some flaws. First, we detected none difference in tail display intensity between two food restriction treatments. This is out of our expectation. We initially assume that two food restriction treatments likely differ in foraging restriction efficiency, and the tail display intensity would be lower in FRO compared with that in FRT. One possible reason is that *P. vlangalii* prefer small insects, which could not be restricted by fishing net added at the bottom of plastic case. In addition, food restriction treatments likely simultaneously restricted lizards' social interaction; thereby evoke the reduction in display intensity. This possibility can be excluded by the lizards' normal territorial defense and display behavior after three days' food restriction treatment.

Conclusion

Our results evidenced that food availability would affect the tail display intensity in *P. vlangalii*. This is the first evidence, as our knowledge, that motion visual signal intensity varies with food availability in lizards. Our study casts an important insight into the honesty of motion visual signal in *P. vlangalii*, suggesting that motion visual signal variation likely reflects the individual quality or resource hold potential, which lays the foundation of signal function during social communication. In following up research, careful design is needed to determine the mechanism behind the tail display weakening under different food availability conditions.

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Xinxin ZHU *et al.*
Variation of Tail Display Intensity
in *Phrynocephalus vlangalii*

No. 3   247

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